VARIATION IN PLANT FUNCTIONAL TRAITS AND VERTICAL STRUCTURE IN HARVESTED FOREST OPENINGS IN THE SOUTHERN APPALACHIANS

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ABSTRACT

VARIATION IN PLANT FUNCTIONAL TRAITS AND VERTICAL STRUCTURE IN HARVESTED FOREST OPENINGS IN THE SOUTHERN APPALACHIANS

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For over two decades, scientists and land managers in the eastern United States have had concerns about the loss of early seral habitat resulting from changes in land use and disturbance regimes. Forest harvest can create early seral habitat within the forested landscape. The size of early seral forest openings and the distance from forest edge can influence microclimate and biotic interactions which affect plant functional traits and vertical structure in openings. This study asks whether there are differences in plant functional traits and vertical structure among openings of different sizes and at different distances from the forest edge. Study sites consisted of eleven shelterwood-harvested openings in the Nantahala National Forest from 2.4 to 13.6 ha in size and five to nine years since harvest, with a range of center-to-edge distances of 29 to 155 m. Openings were grouped into small, medium, and large sizes based on center-to-edge distance, and each opening was divided into concentric zones based on distance from forest edge. Vertical vegetation structure was quantified with mean height of vegetation and foliage height diversity. The woody vegetation was sampled, and shade tolerance, seed mass and wood density values for the community were analyzed to look for differences among opening sizes and opening zones. Vegetation was denser closer to the ground in small openings than in medium and large openings, and no significant differences were found in foliage height diversity for

either opening size or distance from edge. Seed mass was lower in small openings than in medium and large, and at opening centers than edges. Shade tolerance and tree wood density did not differ significantly among opening sizes or zones. Seed mass did display patterns based on opening size and distance from edge, but size and distance from edge were not strong predictors of community-level shade tolerance or tree wood density, or the vertical structure variables measured here. Results suggest that some patterns found may be due to differences in species distribution among study sites. Other factors such as pre-disturbance community and the influence of stump sprouts and leave trees may be affecting community-weighted functional trait means in these openings as well. These results suggest that land managers have a range of sizes to choose from when creating early seral openings and that smaller openings may achieve similar objectives to large openings.

CHAPTER 1: INTRODUCTION

Scientists and land managers have been concerned about the loss of early seral forest habitat and associated wildlife in the eastern United States for more than two decades (Litvaitis 1993; Hunter et al. 2001; Trani et al. 2001; Brooks 2003; Greenberg et al. 2011, King and Schlossberg 2014). This loss is the result of changes in land use and altered disturbance regimes (Lorimer 2001). Natural disturbances that create early seral habitat such as wildfire, flooding, and beavers have been suppressed or removed from ecosystems (Askins 2001). Human activities contributing to the decrease in early seral habitat include fire suppression, abandonment of agricultural lands, and conversion of disturbance-prone forests to non-forest or less disturbance prone conditions (Trani et al. 2001; DeGraaf and Yamasaki 2003; White et al. 2011; King and Schlossberg 2014). Warburton et al. (2011) reported as much as 80% of the forests in the southern Appalachians have moved from early to mid-successional stages.

With the loss of early seral habitat, populations of many early seral habitat specialists have declined to the point where they are now of special management concern and some have gone extinct (Thompson III and DeGraaf 2001; DeGraaf and Yamasaki 2003; King and Schlossberg 2014). Because of these trends, early seral habitat is a management priority where variation in opening size and vegetation structure to accommodate requirements of early seral habitat specialists is being emphasized (Buckner and Shure 1985; Litvaitis 2001; DeGraaf and Yamasaki 2003; Schlossberg and King 2007; Greenberg et al. 2011; King and Schlossberg 2014). Silvicultural treatments to regenerate a new tree cohort can be used as one way to create transient early seral habitats during early stand development (Oliver and Larson 1996; Thompson III and

DeGraaf 2001; DeGraaf and Yamasaki 2003; Loftis et al. 2011).

Early seral forest habitats are generally characterized by a lack of overstory canopy and are dominated by shrubs, vines, young trees, herbs, and grasses (Thompson III and DeGraaf 2001; DeGraaf and Yamasaki 2003; Schlossberg and King 2007; Greenberg et al. 2011; Swanson et al. 2011). Naturally created early seral habitats have higher structural complexity, biological diversity, and food web diversity compared to pre-disturbance forests (Swanson et al. 2011). Canopy removal changes light, temperature, relative humidity, soil moisture, and wind velocity conditions that facilitates a shift in plant and animal species, favoring some species while being less optimal or tolerable for others (Swanson et al. 2011). Vegetation structure and composition differ among early seral forest habitats due to site characteristics, type and severity of natural or anthropogenic disturbance, and biological legacies left behind after disturbance (Franklin et al. 2002; DeGraaf and Yamasaki 2003; Swanson et al. 2011).

Opening size after disturbance can affect environmental conditions as well as biological factors such as seed dispersal (Bradshaw 1992; Davies-Colley et al. 2000; York et al. 2003; Pawson et al. 2006; Baker et al. 2013). Gradients in these factors can also vary with distance from forest edge (forest influence), such as higher light and higher air and soil temperatures farther from the forest edge (Phillips and Shure 1990; York et al. 2003; Shure et al. 2006). Plant functional traits related to photosynthesis, growth, dispersal, and reproduction shift in response to changes in environmental conditions (Westoby 1998; Campetella et al. 2011; Douma et al. 2012; Raevel et al. 2012; Campbell and Donato 2014; Wilfahrt et al. 2014; Craven et al. 2015; Lienard et al. 2015), and thus result in differences in composition, growth rates, primary production, and total biomass of the plant community and the composition of associated non-

plant communities (Buckner and Shure 1985; Phillips and Shure 1990; Litvaitis 2001; Pawson et al. 2006; Shure et al. 2006; King and Schlossberg 2014; Fountain-Jones et al. 2015). While much is known about the characteristics of openings less than 0.5 ha in size (see Muscolo et al. 2014 for review), little published research is available for openings in the range of 2 to 10 ha (Pawson et al. 2006). This study differs from previous studies on early seral openings in the southern Appalachians (Beck and Hooper 1986; Phillips and Shure 1990; Elliott et al. 1997; Elliott et al. 1998; Elliott et al. 2002; Clinton 2003; Berg 2004; Shure et al. 2006) by looking at operationally created openings larger than single tree or group selection size but smaller than previous clearcutting studies and also by focusing on functional traits and vertical structure. The overall purpose of this study was to improve our understanding of how differences in opening size created by operational harvests of 2 to 14 ha are related to characteristics of early seral habitat.

CHAPTER 2: BACKGROUND

Early Seral Forests

Succession is the process of sequential, continuous change in the species of a community, particularly the dominant species, following a major disturbance (Cowles 1899; Clements 1916; Gleason 1926; Clements 1936; Huston and Smith 1987; Huston 1994). A disturbance is a discrete disruption in the structure of a community that results in the sudden death of biomass and changes the environment and resource availability (White and Pickett 1985; Huston 1994). The spatial and temporal scale of disturbance is relative to the dimensions of the community of interest (White and Pickett 1985). Temporally this relates to the life span of organisms, which in forests is often related to the life span of the trees (Huston and Smith 1987). Clements (1916, 1936) proposed the idea of a climax, which he called a "complex organism," that plant communities tended toward by the "stabilizing" process of succession. Others as far back as Cowels (1899) recognized that destabilizing processes kept plant communities from reaching a climax state. Clements focused on the tight relationship of climate and climax, and modern research (Wright and Fridley 2010) has shown that in some ecosystems climate can be a regional driver of the rate of succession.

Stand development is the process of change in forest stand characteristics, including structure and processes (Franklin et al. 2002). The stand development stage following a major disturbance is called stand initiation or cohort establishment, owing to the fact that the disturbance changes the environment sufficiently to allow for the establishment of a new cohort of trees (Oliver and Larson 1996, Franklin et al. 2002). During this stage new plants grow into

the space made available by the death of the overstory, and it is a time of high diversity of plant and animal species (Oliver and Larson 1996). Succession and stand development often happen concurrently, particularly following a major disturbance which can reset succession to an earlier stage and creates conditions for a new tree cohort. The sequence of communities in succession are called seral stages. While it is clear that forest development is a continuous process, it is helpful to recognize certain characteristics of forests in different seral stages (Franklin et al. 2002).

Early seral habitats created by forest harvest are more ephemeral than other woody early seral habitats, and the stand initiation stage only continues as long as the canopy remains open enough to support seedling establishment and ground level vegetation (Oliver and Larson 1996; Thompson III and DeGraaf 2001). The length of time that this period lasts depends on the type of forest community and site conditions, as well as type, intensity, and extent of disturbance (Thompson III and DeGraaf 2001). The next stage of forest structural development, the stem exclusion stage, is characterized by the closing of the canopy, which reduces light reaching the forest floor (Oliver and Larson 1996). These changes also typically mark the transition from early to mid succession.

Much of the forested area in the southern Appalachians was harvested between 1850 and 1920 (White et al. 2011). During this time, intentional burning, grazing, and clearing for agriculture were also widespread in the region (Lorimer 2001; White et al. 2011). Fire suppression and abandonment of agricultural lands along with maturation of these forests led to a decrease in early seral habitat throughout the eastern United States including the southern Appalachians (Trani et al. 2001; DeGraaf and Yamasaki 2003). In National Forests in the

southern Appalachians, the proportion of forest less than 10 years old has decreased from 5% in the 1980s and 1990s to just above 1% in 2011 (Warburton et al. 2011).

Several animal species have been identified as early seral specialists that have requirements for early seral structural characteristics, minimum opening size, or both (Buckner and Shure 1985; Litvaitis 2001; Schlossberg and King 2007; King and Schlossberg 2014). Some structural characteristics important for wildlife are height and vertical profile of vegetation, patchiness, diameter and density of stems, and proportion of cover between woody and herbaceous plants (Litvaitis 2001; Schlossberg et al. 2010; King and Schlossberg 2014). The loss of early seral forests in the eastern United States has led to greater attention from the scientific and land management communities and an effort to understand and manage for the conservation of these habitats and the associated species.

Vertical Structure and Plant Functional Traits

Structure in a forest refers to both the individual structures in the forest and also their spatial arrangement (Franklin et al. 2002). Understanding structure is important because this can be most directly manipulated, can be measured and used as a surrogate for functions or organisms that are more difficult to measure directly, and structures have direct value in themselves as products, such as wood, or as services, such as carbon sequestration (Franklin et al. 2002).

Vertical structure is the layering of foliage (Brokaw and Lent 1999). This can happen by growth form layers (forbs, shrubs, trees) or by a range of heights of one form such as understory and overstory trees, or ground cover and tall forbs. Vertical structure can be measured by the mean height of foliage, a profile of the foliage from the ground up, or with other more indirect

measures like foliage height diversity (MacArthur and MacArthur 1961; Aber 1979; Brokaw and Lent 1999). The vertical structure of a forest changes through time, not only with initially increasing the height of vegetation but also with changes in the vertical spacing and clumping of vegetation over time (Aber 1979). Vertical structure has a direct impact on vertebrate and invertebrate communities with some species showing clear preferences for certain layers, arrangement, or particular structures (Buckner and Shure 1985; Morimoto and Wasserman 1991; Fountain-Jones et al. 2015). Researchers have also shown the association of vertical structural measures, such as foliage height diversity, with bird species richness and the helpfulness of including these measures in models (MacArthur and MacArthur 1961; Clawges et al. 2008; Culbert et al. 2013; Huang et al. 2014).

Three plant functional traits related to succession are shade tolerance, seed mass, and wood density (Valladares and Niinemets 2008; Wilfahrt et al. 2014). Shade tolerance, long recognized as important to forest development and management (Baker 1949) is the ability of plants to grow under reduced light conditions, typically in the shade of other plants (Givnish 1988; Valladares and Niinemets 2008). Shade intolerant species generally outcompete more tolerant species early on in succession and then are gradually replaced by more shade tolerant species (Valladares and Niinemets 2008; Lienard et al. 2015). Lienard et al. (2015) reported that shade tolerance is an important driver of succession in some regions of the US, but may not be as an important of a driver in other regions, one of which includes the southern Appalachians. Kern et al. (2013) found that the shade tolerance of ground level vegetation, including woody vegetation up to 0.5 m tall, decreased from the smallest (6 m in diameter) to largest (43 m in diameter) openings and also was lowest in the center of openings. Shade tolerant species have

been shown to have lower relative growth rates and seed mass than less tolerant species (Reich et al. 1998). In the southern Appalachians, some shade intolerant species have been found to dominate forest opening biomass through sprouting (Phillips and Shure 1990; Shure et al. 2006).

Within a plant community, seed mass can vary by multiple orders of magnitude and is often log-normally distributed (Moles and Westoby 2006). Differences in seed mass are generally small within genera and even within taxonomic families (Leishman and Westoby 1995). Seed mass is thought to be a trade-off between competing reproductive strategies of producing few large seeds or many small seeds, and the range of seed sizes found within single plant communities shows that both strategies can be present in the same environment (Moles and Westoby 2006). Some researchers have found correlations between seed mass and successional stage, with lower mean seed mass earlier in succession and higher mean seed mass in later succession (Campetella et al. 2011; Wilfahrt et al. 2014). However, Schweinbacher et al. (2012) did not find a correlation between seed mass and successional stage in a study of succession following glacial retreat. There is some evidence that heavier-seeded species have higher establishment rates in shade than lighter-seeded species, but after the initial resources from the seed are consumed, it is not clear that heavier-seeded species have higher survival in shade than lighter-seeded species (Saverimuttu and Westoby 1996; Moles and Westoby 2006). Heavier-seeded young plants may have more time to capitalize on a stochastic change from a shady to more open light environment than lighter seeded species in the same environment (Saverimuttu and Westoby 1996).

Seed mass also relates to dispersal, with lighter seeds often being wind-dispersed or unassisted and heavier seeds being dispersed by vertebrates (Westoby et al. 1996). In a study of

wind-dispersed seeds, Greene and Johnson (1993) found that lighter seeds fall slower and thus may disperse farther, but Thomson et al. (2011) conducted a meta-analysis of 140 species across growth forms and found that within dispersal mode seed mass did not correlate with dispersal distance. Instead, plant height was the strongest predictor of dispersal distance, and when plant height was controlled for, lighter seeds did have longer dispersal distances, but the correlation was weak. Differences in seed dispersal related to distance from forest edges into openings have been found (Tabor et al. 2007). Holladay et al. (2006) found that seedlings of wind-dispersed trees were more prevalent in opening centers (largest size 40 m in diameter) than animal-dispersed trees, such as oaks; animal-dispersed seedlings were more prevalent in the adjacent forest; and opening edges had a mix of the two.

Wood density has been found to be a trade-off between strength and hydraulic properties (Chave et al. 2009; Lachenbruch and McCulloh 2014). Denser wood is stronger and can resist forces that would break the stem, but less dense wood has greater conductance of water (Swenson and Enquist 2007; Lachenbruch and McCulloh 2014). Denser wood is also less prone to embolism or rupture and thought to help with drought tolerance (Ackerly and Cornwell 2007; Swenson and Enquist 2007; Chave et al. 2009). In tropical forest seedlings, Augspurger (1984) found that more shade tolerant species had denser wood. Wood density relates to growth in that usually faster growing species have less dense wood (King et al. 2005; Swenson and Enquist 2007) although this is not always true (Chave et al. 2009).

CHAPTER 3: MANUSCRIPT
VARIATION IN PLANT FUNCTIONAL TRAITS AND VERTICAL STRUCTURE IN HARVESTED FOREST OPENINGS IN THE SOUTHERN APPALACHIANS

Introduction

Environmental conditions of early seral forests differ from other stages of forest succession due to the removal of the overstory canopy (Swanson et al. 2011). Early seral forests typically have increased sunlight on the forest floor; more extreme temperatures; lower relative humidity, surface soil moisture, and litter moisture; and higher wind velocities (Phillips and Shure 1990; Davies-Colley et al. 2000; Swanson et al. 2011; Baker et al. 2014b). Opening size affects the environmental conditions in early seral openings (York et al. 2003; Pawson et al. 2006; Shure et al. 2006), with, for example, higher light levels and soil and air temperatures in larger openings (Phillips and Shure 1990). Openings greater than 0.10 ha can have microclimates different from smaller openings (Schliemann and Bockheim 2011) which has an impact on ecosystem processes and the plant and animal species that will colonize or use the opening (Swanson et al. 2011). Shure et al. (2006) found that when forest openings in the southern Appalachians increase from 0.02 to 2.0 ha, net primary productivity, biomass, and stem density increase for several years after disturbance.

Species with all levels of shade tolerance were found in large openings (9 to 59 ha) in the southern Appalachians, but shade intolerant species tend to dominate in terms of abundance and biomass (Beck and Hooper 1986; Elliott et al. 1997; Elliott et al. 1998; Elliott et al. 2002). The minimum gap size for recruitment of shade intolerant species has been shown to be in the range of 0.04 to 0.10 ha (Whitmore 1982; Busing 1994), and smaller gaps favor shade tolerant species (Muscolo et al. 2014). Other functional traits shown successional patterns as well. Wilfahrt et

al. (2014) concluded that early seral forests have lower seed mass and less dense wood than older forests. Greater vertical structural complexity and denser vegetation in the ground and shrub layers have also been associated with early seral habitats (Aber 1979; Clawges et al. 2008; Culbert et al. 2013; Huang et al. 2014). Larger openings up to 1.0 ha had higher tree growth rates than smaller openings (York et al. 2003; York et al. 2004). Bruckner and Shure (1985) reported higher foliage height diversity (a measure of vertical heterogeneity) in larger openings up to 10.0 ha.

Distance from forest edge has also been shown to affect the microclimate of early seral forests with increasing light, air temperature, and soil temperature, and decreasing humidity with farther distance from the forest edge (Phillips and Shure 1990; Baker et al. 2014b; Baker et al. 2016). This forest influence, the effect of the intact forest on the disturbed area, has been linked to patterns of seed dispersal as well as changes in the composition of plant and arthropod communities with a decreasing influence with increased distance from forest edge (Tabor et al. 2007; Baker et al. 2014a; Fountain-Jones et al. 2015). Forest influence affects structure as well. Reduced light and soil resources at opening edges were linked to suppression of young tree growth in openings as large as 1.0 ha (York et al. 2003; York et al. 2004).

Little has been published about differences in plant functional traits and vertical structure based on opening size and distance from forest edge in openings larger than 0.5 ha. The objective of this study was to determine if shade tolerance, seed mass, tree wood density, and vertical structure varied based on opening size and distance from edge in early seral openings of 2.0 to 14.0 ha, created by operational harvest methods. I expected shade tolerance, seed mass, and wood density to decrease with increased opening size and farther distance from edge because

of microclimate differences such as increased light in larger openings and at opening centers and higher wind speeds in larger openings. I also expected vertical vegetation structure to be more diverse and have a taller mean height in larger openings than in smaller ones and at opening centers than at edges because of increased light in larger openings and at opening centers.

Methods

Study Sites and Design

Data were collected from July to October 2015 in eleven openings created via timber harvesting in the Nantahala National Forest, Graham County, North Carolina, USA (Fig. 1, Table 1). Study openings ranged from 2.4 to 13.6 ha and were logged between 2006 and 2009 using a shelterwood with reserves (i.e., two-aged) regeneration method. Approximately 4.5 m^2/ha of basal area was left, with leave trees favoring hard mast producing species (*Quercus* L., *Carya* Nutt., *Aesculus* L.). Openings also had herbicide applied to woody stumps within three years of harvest. All openings were mixed-hardwood stands classified by the US Forest Service (USFS) as *Liriodendron tulipifera* L.—*Quercus alba* L.—*Quercus rubra* L. forest type (Eyre 1980). Slopes ranged from 0 to 90% with a mean of 48%. Elevation within study sites ranged from 550 to 1140 m.

For each opening, the edge was determined initially using GIS outlines of the harvested areas from USFS maps and updated with GPS points taken in the field. Opening edges were defined in the field by locating the outermost cut stumps. A centroid for each opening was created in ArcMap 10.2 (ESRI 2014) and the shortest distance from the centroid to the GIS perimeter of the opening was established as the center-to-edge distance.

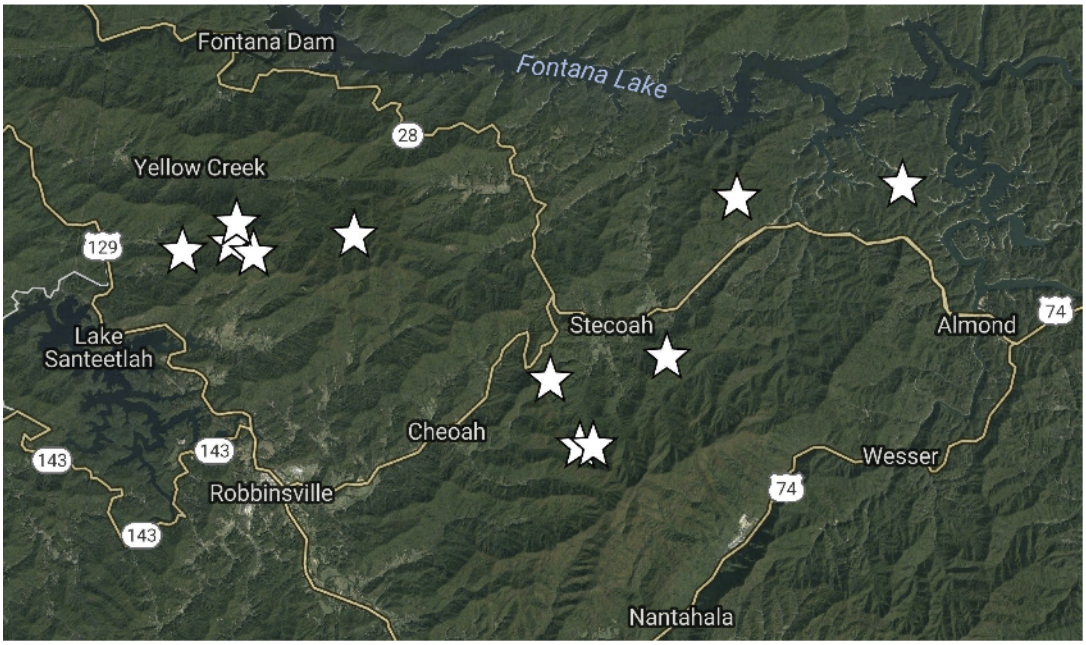

Figure 1. Location of field sites (stars) in the Nantahala National Forest, Graham County, North Carolina. Map data by Google (2017).

Table 1. Characteristics of harvested openings studied in Nantahala National Forest, Graham County, North Carolina.

Opening size	Center-to-edge distance (m)	Area (ha)	Opening shape	Yrs since harvest	# of plots	Mean elevation (m)	Mean slope (%)	Mean aspect (deg.)
Small	29	2.4	Long irregular	6	14	633	46	78
Small	40	2.8	Long irregular	6	18	587	33	328
Small	45	4.0	Circle regular	8	13	908	53	118
Medium	75	7.6	Circle irregular	5	12	1048	52	305
Medium	75	11.6	Long irregular	8	16	891	49	207
Medium	90	9.6	Long irregular	8	20	1030	36	340
Medium	100	13.6	Long irregular	8	20	822	66	319
Large	118	10.0	Irregular	9	19	1125	48	301
Large	120	9.2	Triangle regular	9	21	1052	40	264
Large	140	8.0	Circle irregular	8	25	972	45	62
Large	155	9.2	Square regular	8	22	982	56	57

Openings were grouped into small, medium, and large classes based on center-to-edge distance. This measure was used, rather than opening area, to account for opening size because of the irregular shapes of the openings. For example, a narrow rectangular opening may have a larger area than a roughly circular opening but may have a shorter center-to-edge distance. Because forest influence on microclimate and biotic factors such as seed dispersal can change with distance from the edge (Davies-Colley et al. 2000; York et al. 2003; Tabor et al. 2007; Baker et al. 2013; Baker et al. 2014b), using center-to-edge distance allowed openings to be classified into groups with similar edge effects. Small openings had a center-to-edge distance of 29 to 45 m, medium openings had a center-to-edge distance of 75 to 100 m, and large openings had a center-to-edge distance of 118 to 155 m (Table 1). These groupings were decided on post-hoc based on both the separation between center-to-edge distances and because they formed three groups on nearly equal size.

Data Collection

Data were collected in 9 m^2 plots (3 m x 3 m) nested within transects running along the short and long axes of openings toward the centroid (Fig. 2). Openings contained two transects if roughly circular or square shaped or three transects if oblong or rectangular shaped. The additional transect was added to these latter openings in an attempt to avoid under-sampling. In smaller openings, plots were spaced 10 m apart along transects. In larger openings, 15 m spacing was used to make the sample size approximately the same in different sized or shaped openings. Because openings varied in size and shape, effects of distance from edge were analyzed by grouping plots into three "opening zones" based on proportional distance from edge. To obtain the proportional distance from edge, the actual distance from the forest edge for each plot was

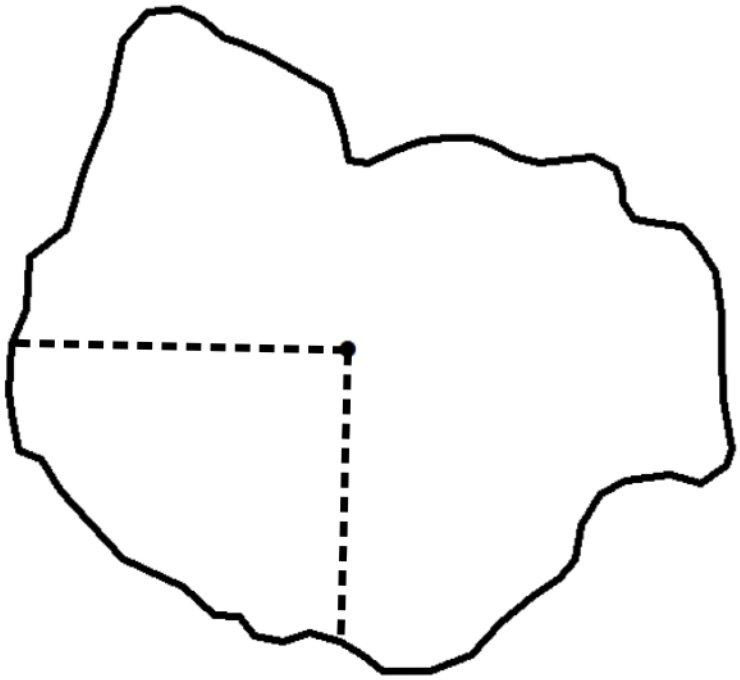

Figure 2. Example of transect layout for an opening. Solid line is opening boundary and dashed lines are transects

was from 0 to 33.3% of the center-to-edge distance, the “mid-way” zone was 33.4 to 66.6%, and the “center” zone was 66.7 to 100%. Because zones are based on proportional distance, the actual distance from the edge for the boundaries of each zone is different for each opening. Therefore, the mean distance of the plots within a zone is different among size groups (Table 2).

Slope at each plot was measured in percent using a clinometer, aspect of the slope was measured in degrees using a compass, and elevation was measured using a Garmin 62 GPS unit. Within each 9 m^2 plot, the count by species of all woody stems and their diameters were recorded. Stems of clonal species were measured separately if they were separate at ground level. Diameter at 1.3 m above groundline (dbh) was recorded for stems greater than 2.5 cm dbh. Diameter of stems less than 2.5 cm dbh was measured 5 cm above groundline. Stem density and mean stem diameter were calculated for each plot and included all stems. These plot level values were used to calculate a mean stem density and mean stem diameter for each opening size group. Species diversity (Shannon's diversity index: $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of total stems of species i) was calculated for each zone within each opening and means were calculated for each opening size.

Vertical vegetation structure was measured at each plot by counting the number of contacts live vegetation made along a 5 m tall pole within six height classes: 0 to 0.5 m, 0.5 to 1 m, and in 1 m segments from 1 to 5 m. Vegetation above 5 m only occurred from leave trees left during harvesting and was thus not included. Two vertical structure samples were measured on both sides of each plot along the transect to better describe the vegetation structure. Vegetation structure was compared among opening sizes and distance from the edge based on mean number of contacts in each height class, mean vegetation height, and foliage height diversity (FHD), a

Table 2. Mean distance from forest edge for the sample plots in each zone for each opening size group. Zones are based on percentage of center-to-edge distance: edge zone = 0-33.3%, mid-way zone = 33.4-66.6%, and center zone = 66.7-100%.

	Mean distance from edge (m) of plots in zone		
Opening Size	Edge	Mid-way	Center
Small	4.7 (N=15)	18.7 (N=11)	32.1 (N=19)
Medium	12.8 (N=25)	45.9 (N= 17)	77.0 (N=26)
Large	20.3 (N=34)	68.0 (N=27)	115.9 (N=26)

measure of vertical heterogeneity (MacArthur and MacArthur 1961). The mid-point of the height range was used as the height of each contact to calculate mean vegetation height. FHD was calculated using Shannon's diversity index: $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of total contacts in height class i.

Species values for shade tolerance, seed mass, and wood density for each woody species were based on available literature and databases (see Appendix A for data sources). Shade tolerance was based on the 0 to 5 scale in Niinemets and Valladares (2006) where 0 is no tolerance and 5 is maximal tolerance. If a species was not part of the data set in Niinemets and Valladares (2006), the USDA PLANTS database (USDA, NRCS) was used, and intolerant species were given a value of 2, intermediate species a value of 3, and tolerant species a value of 4. For seed mass, where data were not available for a species, a similar congeneric or group of congeneric species was used (indicated in Appendix A).

Data Analysis

A split-plot design was used to study the influence of opening size and distance from opening edge (opening zones) on vertical structure and functional trait variables. Main plots were the small, medium, and large opening sizes. Opening zones formed the split-plot. An individual opening was considered the experimental unit.

A linear mixed model (R function “lmer”, “lme4” package [Bates et al. 2015]) was used to test for the effect of opening size and opening zone on vertical structure (mean vegetation height and FHD) and functional trait variables (shade tolerance, seed mass, and wood density). Opening size and zone were analyzed as fixed factors and opening was included as a random factor. F-values were used to test for significance of fixed factors at a $p < 0.05$ level of

significance with the p-values provided by the R package "lmerTest" (Kuznetsova et al. 2016) using Satterthwaite's approximation to degrees of freedom. When a factor was significant, differences among factor-levels were tested using differences of least squares means (R function "difflsmeans", "lmerTest" package (Kuznetsova et al. 2016)). All the statistical analyses were performed using R Core Team (2017).

Stems greater than 8 cm dbh were excluded from all analyses of plant functional traits because they were considered leave trees left by the shelterwood harvest. Dry seed mass (mg) values were log-transformed before analyses to meet assumptions of normality, because seed mass within communities has been shown to be log-normally distributed (Moles and Westoby 2006). Because of a lack of available data for wood density of shrub species, only tree species data were used in analyses of wood density.

Due to lack of functional trait data, species excluded from shade tolerance analyses were *Aristolochia durior* Hill, *Rhododendron calendulaceum* (Michx.) Torr., *Ilex montana* Torr. & Gray*, and Euonymus obovatus* Nutt., those excluded from the seed mass analyses were *Aristolochia durior* and *Rhododendron calendulaceum,* and those excluded from wood density analyses were *Cornus alternifolia* L. f.*, Asimina triloba* L*,* and *Ilex montana*. Total abundance of excluded species was a small fraction of the data sets they were excluded from.

Results

Site Character

Acer rubrum L. was the most common tree (by count) in small and medium openings, and *Liriodendron tulipifera* was the most common in large openings (Table 3). Tree species common in medium openings were also typically common in both of the other sizes. Small and

Table 3. Ten most numerous tree species for each opening size by stem count. Stem area is total stem cross-sectional area in all plots of that size category. Maximum number of plots for small openings = 45, medium = 68, and large = 87.

Opening size	Tree species	Shared[a]	Stem count	Stem area (cm^2)	% of plots
Large	*Liriodendron tulipifera* L.	SML	156	261.70	37
	Quercus rubra L.	ML	127	126.68	42
	Acer rubrum L.	SML	83	220.37	34
	Betula lenta L.		73	269.37	17
	Halesia tetraptera Ellis	ML	71	308.02	33
	Fraxinus spp. L.		62	223.23	31
	Quercus montana Willd.	ML	57	2.06	10
	Tilia americana L.	ML	57	509.00	17
	Ilex montana Torr. & A. Gray ex A. Gray		45	179.67	10
	Acer saccharum Marshall		41	148.84	7
Medium	*Acer rubrum* L.	SML	254	446.28	48
	Quercus rubra L.	ML	200	307.07	47
	Quercus montana Willd.	ML	187	51.16	23
	Halesia tetraptera Ellis	ML	78	339.63	25
	Liriodendron tulipifera L.	SML	70	224.56	32
	Carya glabra (Mill.)	SM	45	65.91	30
	Nyssa sylvatica Marshall	SM	39	151.42	22
	Sassafras albidum (Nutt.) Nees	SM	38	75.12	17
	Quercus alba L.	SM	36	5.30	7
	Tilia americana L.	ML	36	314.69	13
Small	*Acer rubrum* L.	SML	101	273.43	25
	Quercus coccinea Münchh.		86	100.85	18
	Quercus species. L.		59	0.46	8
	Nyssa sylvatica Marshall	SM	47	161.75	21
	Sassafras albidum (Nutt.) Nees	SM	46	52.05	14
	Quercus alba L.	SM	31	51.47	11
	Oxydendrum arboreum (L.) DC.		27	210.44	7
	Carya glabra (Mill.)	SM	22	64.42	11
	Liriodendron tulipifera L.	SML	17	86.53	7
	Quercus falcata Michx.		17	169.49	6

[a]Species is in ten most numerous by count for small, medium, and large (SML), small and medium (SM), or medium and large (ML) openings.

large openings each had a few common species that were not common in the other sizes. For example, *Quercus coccinea* Münchh. was common in small openings but not in medium or large openings. *Betula lenta* L. and *Fraxinus* species L. were common in large openings, but not in the other sizes. *Quercus rubra* was common in medium and large openings but not in small.

Overall, there was considerable overlap of the most common shrubs (by count) among opening sizes, but large and medium openings had more overlap with each other than did small with medium and large (Table 4). *Rubus allegheniensis* Porter, *Rubus canadensis* L., and *Gaylussacia ursina* (M.A. Curtis) Torr. & A. Gray ex A. Gray were common in medium and large openings. Ericaceous shrubs including *G. ursina, Vaccinium* species L., *Gaultheria procumbens* L., and *Kalmia latifolia* L. were common in small openings. *Smilax rotundifolia* L. and *Hydrangea arborescens* L. were common in all opening sizes, although, *H. arborescens* decreased in presence from large to small openings.

Mean stem density (stems/m^2) in openings was 7.2 (SE=0.62), 4.3 (SE=0.21), and 2.7 (SE=0.15), in small, medium, and large openings, respectively. Mean stem diameter in openings was 0.7 (SE=0.06) cm, 1.0 (SE=0.06) cm, and 1.4 (SE=0.10) cm in small, medium, and large openings, respectively. Species diversity (H') in openings was 1.96 (SE=0.16), 2.56 (SE=0.06), and 2.43 (SE=0.09) in small, medium, and large openings, respectively.

Vertical Vegetation Structure

The vertical vegetation distributions for medium and large openings were similar (Fig. 3), while small showed denser vegetation up to 1 m. Mean vegetation height and FHD did not differ significantly among sizes or zones (Figs. 4-7, Table 5). There was also no significant interaction between size and zone for either mean vegetation height or FHD (Appendix B).

Table 4. Ten most numerous shrub species for each opening size by stem count. Stem area is total stem cross-sectional area in all plots of that size category. Maximum number of plots for small openings = 45, medium = 68, and large = 87.

Opening size	Shrub species	Shared[a]	Stem Count	Stem area (cm^2)	# of plots
Large	*Hydrangea arborescens* L.	SML	281	36.90	60
	Rubus allegheniensis Porter	ML	143	30.53	33
	Rubus canadensis L.	ML	141	32.04	29
	Pyrularia pubera Michx.	ML	127	121.54	20
	Gaylussacia ursina (M.A. Curtis) Torr. & A. Gray ex A. Gray	SML	81	4.37	4
	Smilax rotundifolia L.	SML	62	4.22	22
	Calycanthus floridus L.	SML	53	56.77	9
	Vitis spp. L.		37	82.67	21
	Viburnum acerifolium L.	ML	29	4.09	9
	Rhododendron calendulaceum (Michx.) Torr.	ML	28	44.16	2
Medium	*Smilax rotundifolia* L.	SML	311	26.91	51
	Hydrangea arborescens L.	SML	148	20.21	34
	Rubus allegheniensis Porter	ML	144	36.81	25
	Pyrularia pubera Michx.	ML	139	80.88	22
	Calycanthus floridus L.	SML	138	46.02	14
	Gaylussacia ursina (M.A. Curtis) Torr. & A. Gray ex A. Gray	SML	132	7.26	12
	Viburnum acerifolium L.	ML	83	50.46	13
	Rubus canadensis L.	ML	64	4.32	13
	Vaccinium pallidum Aiton	SM	47	4.66	9
	Rhododendron calendulaceum (Michx.) Torr.	ML	41	34.16	13
Small	*Gaylussacia ursina* (M.A. Curtis) Torr. & A. Gray ex A. Gray	SML	1120	96.08	32
	Gaultheria procumbens L.		422	3.64	17
	Vaccinium pallidum Aiton	SM	277	20.22	22
	Hydrangea arborescens L.	SML	144	32.58	11
	Smilax rotundifolia L.	SML	131	8.31	36
	Calycanthus floridus L.	SML	54	52.06	7
	Kalmia latifolia L.		37	61.48	6
	Symplocos tinctoria (L.) L'Hér.		37	50.40	10
	Vaccinium stamineum L.		31	39.20	8
	Smilax glauca Walter		26	0.91	16

[a]Species is in ten most numerous by count for small, medium, and large (SML), small and medium (SM), or medium and large (ML) openings.

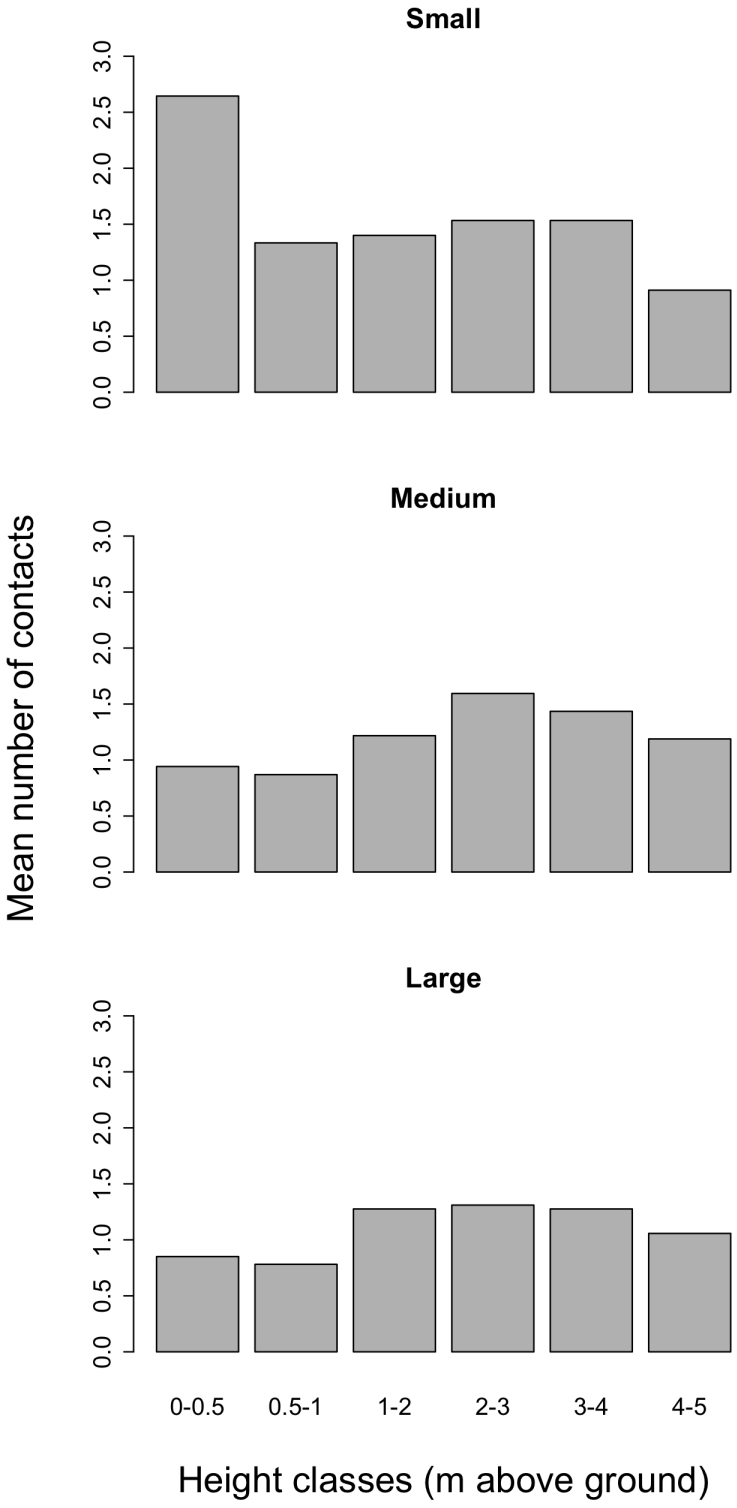

Figure 3. Vertical vegetation distributions for openings of different sizes.

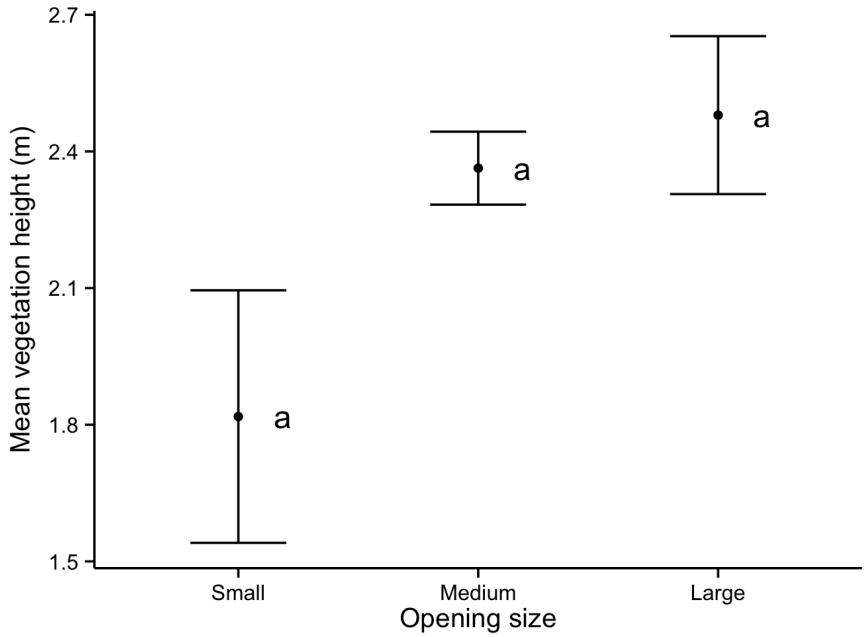

Figure 4. Mean vegetation height by opening size. Letters indicate significant differences. Bars are ± SE.

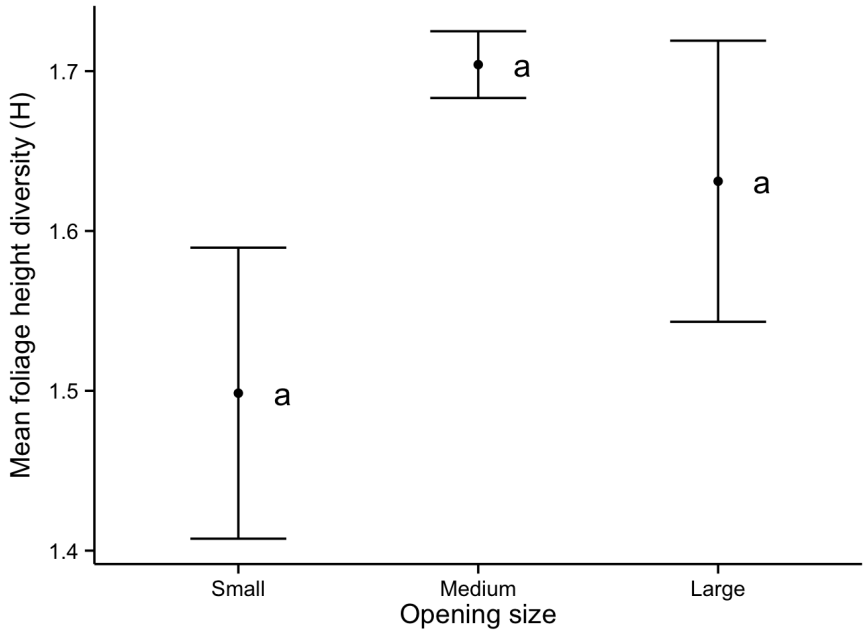

Figure 5. Mean foliage height diversity (H') inside openings by opening size. Letters indicate significant differences. Bars are ± SE.

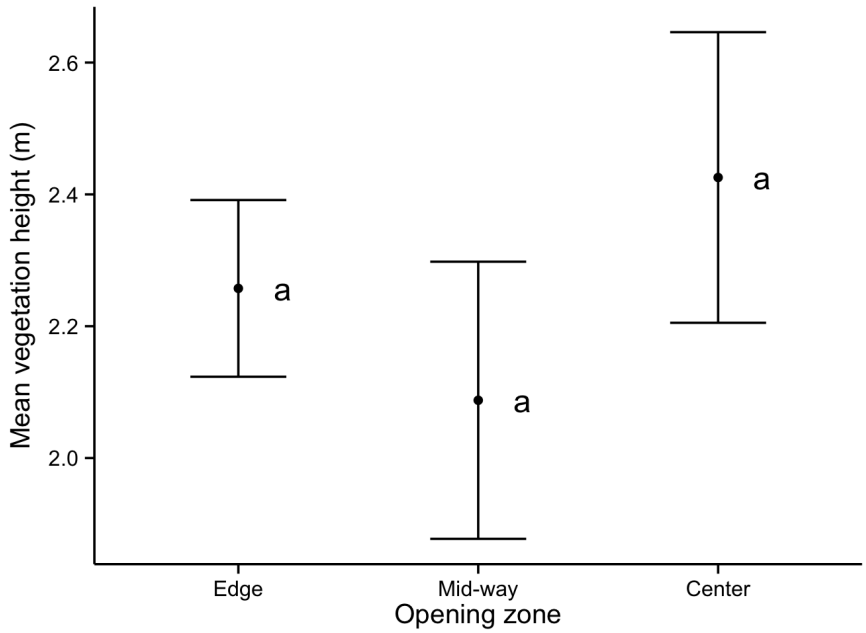

Figure 6. Mean vegetation height by opening zone. Letters indicate significant differences. Bars are ± SE.

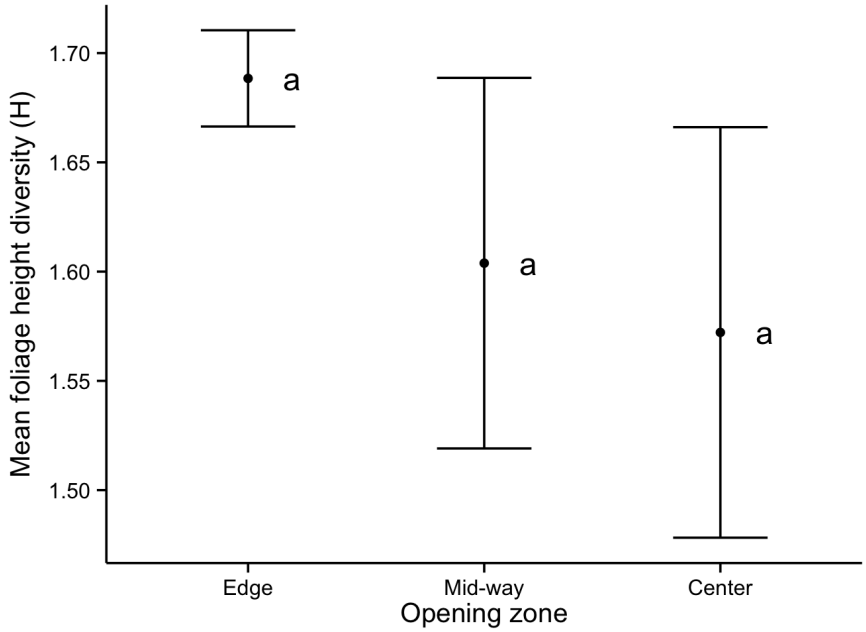

Figure 7. Mean foliage height diversity (H') by opening zone. Letters indicate significant differences. Bars are ± SE.

Table 5. Mean values (±SE) of functional traits and vertical structure variables for opening sizes and opening zones with P-values and F-values from linear mixed models.[a]

	Opening size					Opening zone				
	Small	Medium	Large	P	F (df: 2,8)	Edge	Mid-way	Center	P	F (df: 2,16)
Shade tolerance[b]										
All species	2.93±0.05	2.88±0.08	3.00±0.08	0.7634	0.27936	2.96±0.09	2.93±0.08	2.93±0.05	0.9524	0.04887
Trees	2.77±0.06	2.95±0.05	3.03±0.10	0.2605	1.59872	2.93±0.09	2.97±0.09	2.90±0.06	0.7569	0.28347
Shrubs	2.99±0.06	2.79±0.12	3.01±0.08	0.5878	0.56821	2.96±0.11	2.88±0.11	2.93±0.08	0.5975	0.53191
Seed mass (log_{10}mg)										
All species	0.50±0.13	1.60±0.10	1.19±0.14	0.0148	7.4621	1.31±0.18	1.17±0.18	0.98±0.19	0.0308	4.3567
Trees	2.36±0.12	2.30±0.11	2.12±0.11	0.4149	0.98407	2.25±0.15	2.30±0.10	2.20±0.09	0.7694	0.26648
Shrubs	-0.08±0.07	0.93±0.12	0.41±0.20	0.0555	4.2408	0.63±0.21	0.47±0.20	0.29±0.16	0.0403	3.9496
Wood density (g/cm^3)										
Trees	0.52±0.007	0.51±0.007	0.50±0.010	0.4701	0.83078	0.51±0.006	0.51±0.010	0.51±0.009	0.8122	0.21071
Vertical structure										
Mean height (m)	1.8±0.28	2.4±0.08	2.5±0.17	0.3093	1.3637	2.3±0.13	2.1±0.21	2.4±0.22	0.1284	2.3772
FHD (H')	1.50±0.09	1.70±0.02	1.63±0.09	0.2818	1.48997	1.69±0.02	1.60±0.08	1.57±0.09	0.4054	0.95575

[a] See Appendix B for full ANOVA tables.

[b] Shade tolerance is measured on a 0-5 scale (0 is lowest, 5 highest) created by Niinemets and Valladares (2006).

Plant Functional Traits

Shade tolerance did not differ significantly among opening sizes or zones for all species, trees, or shrubs (Figs. 8 and 9, Table 5). There were no significant interactions between opening size and zone for shade tolerance of all species, trees, or shrubs (Fig. 10). Seed mass was significantly lower in small than in medium and large openings (Fig. 11, Table 5), but did not differ among sizes when trees and shrubs were considered separately (Fig. 11, Table 5). Seed mass was significantly higher at the edge than at the center of openings for all species and shrubs (Fig. 12, Table 5). Seed mass for trees only did not differ significantly among zones (Fig. 12, Table 5). There were no significant interactions between size and zone for seed mass (Fig. 13). Wood density did not differ significantly among opening sizes or zones (Figs. 14 and 15, Table 5) and there was no significant interaction between size and zone (Fig. 16).

Discussion

Differences in light due to forest influence led me to expect taller vegetation in large than in small openings and at opening centers than at edges (York et al. 2003; Baker et al. 2014b). Additionally, in a study comparing openings of different sizes in the southern Appalachians, Phillips and Shure (1990) found higher production and biomass in opening centers than edges. However, I found no significant differences in mean height among opening sizes or zones. It is possible that the increased production associated with opening centers leads to more competition, limiting height growth. The amount of variation around the mean in small openings (SE = 0.28 m) may be masking a difference in mean height based on opening size, as the mean is lower in small openings than medium and large, but the difference is not statically significant. Buckner and Shure (1985) found FHD up to 2 m above ground in southern Appalachian forests increased

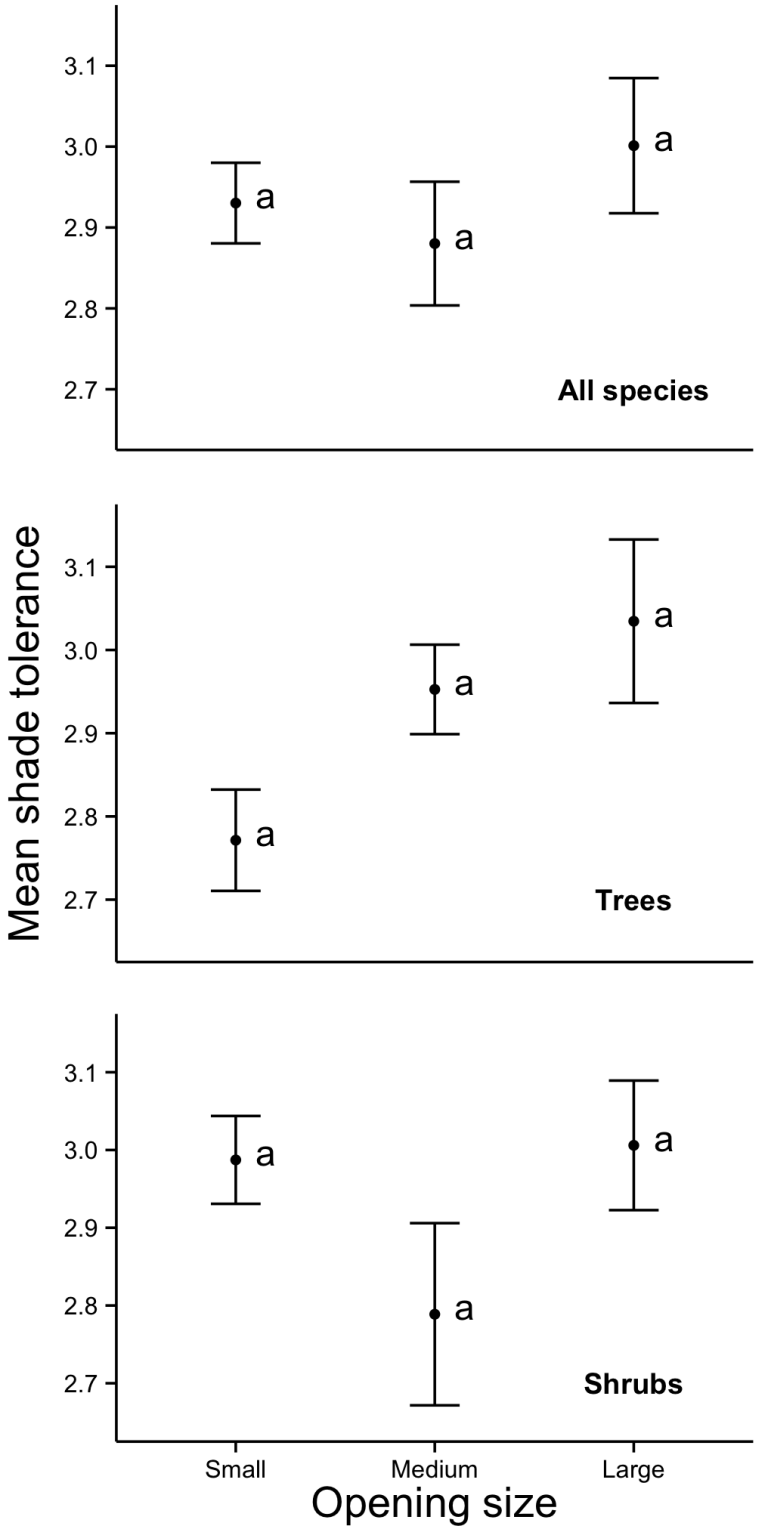

Figure 8. Mean shade tolerance (0-5 scale, 0 is lowest tolerance, 5 highest) by opening size. Letters indicate significant differences. Bars are ± SE.

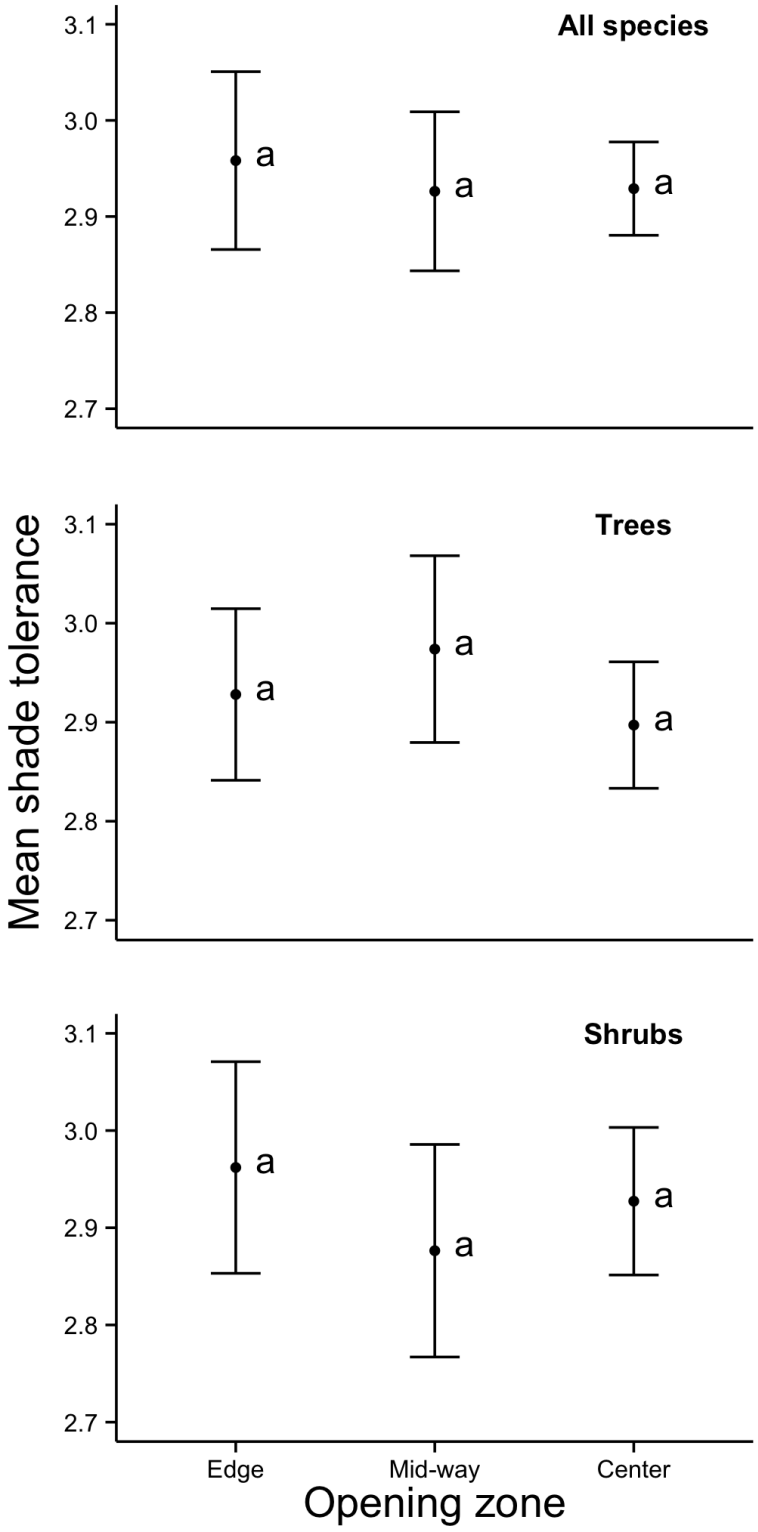

Figure 9. Mean shade tolerance (0-5 scale, 0 is lowest tolerance, 5 highest) by opening zone. Letters indicate significant differences. Bars are ± SE.

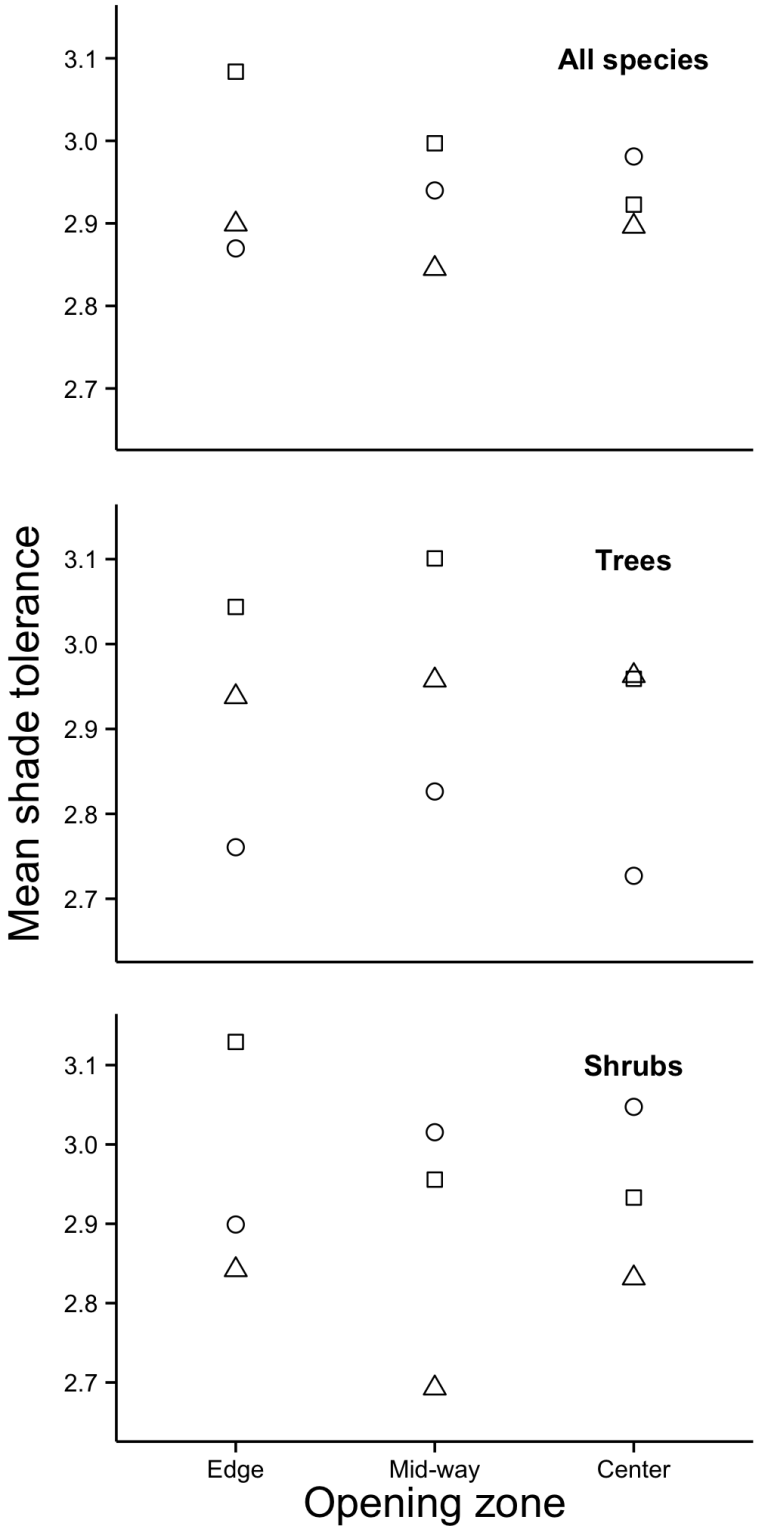

Figure 10. Mean shade tolerance (0-5 scale, 0 is lowest tolerance, 5 highest) by opening zone and size. Shapes are means of different opening sizes. Circles are small openings, triangles are medium, and squares are large.

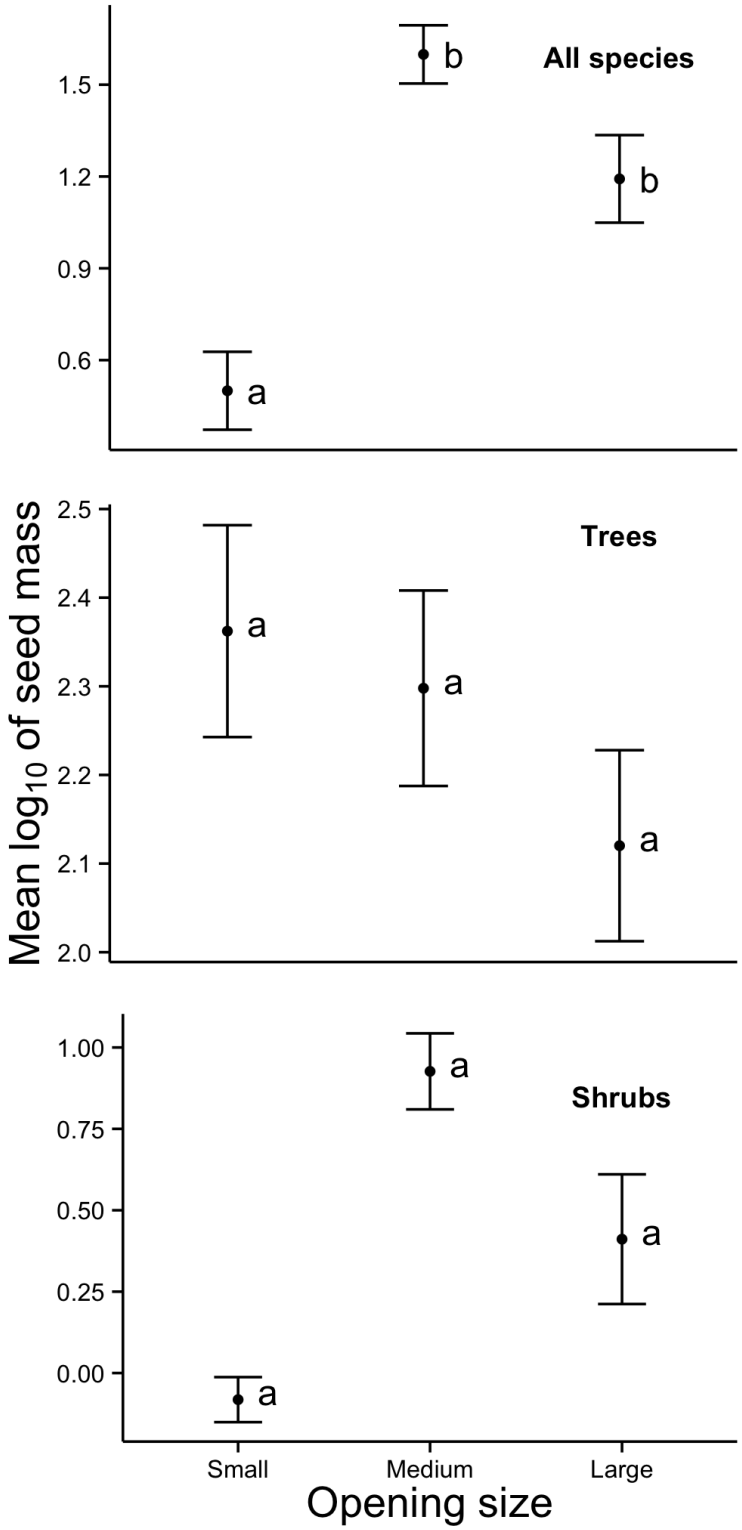

Figure 11. Mean $\log_{10}$ of seed mass by opening size. Letters indicate significant differences. Bars are ± SE.

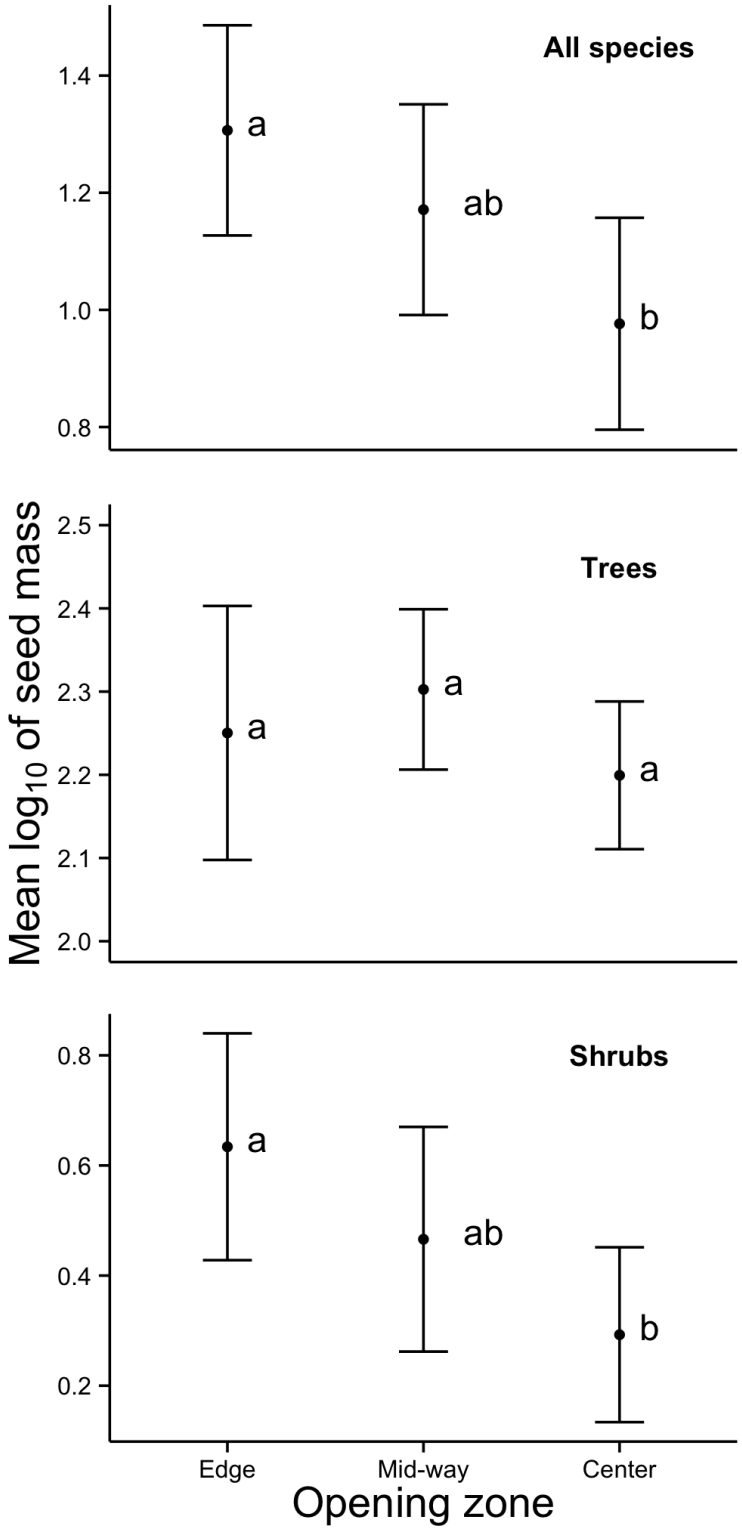

Figure 12. Mean $\log_{10}$ of seed mass by opening zone. Letters indicate significant differences. Bars are ± SE.

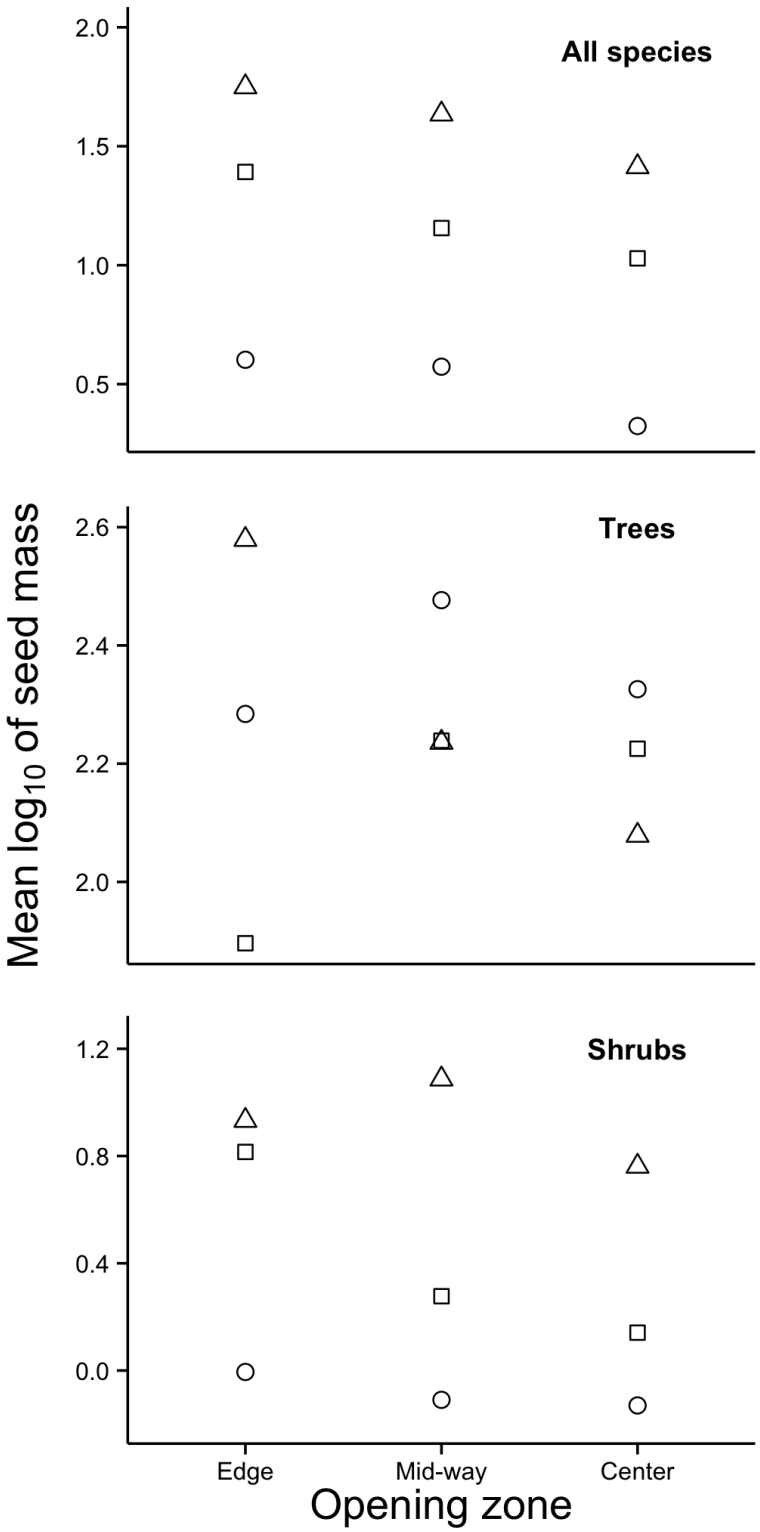

Figure 13. Mean $\log_{10}$ of seed mass by opening zone and size. Shapes are means of different opening sizes. Circles are small openings, triangles are medium, and squares are large.

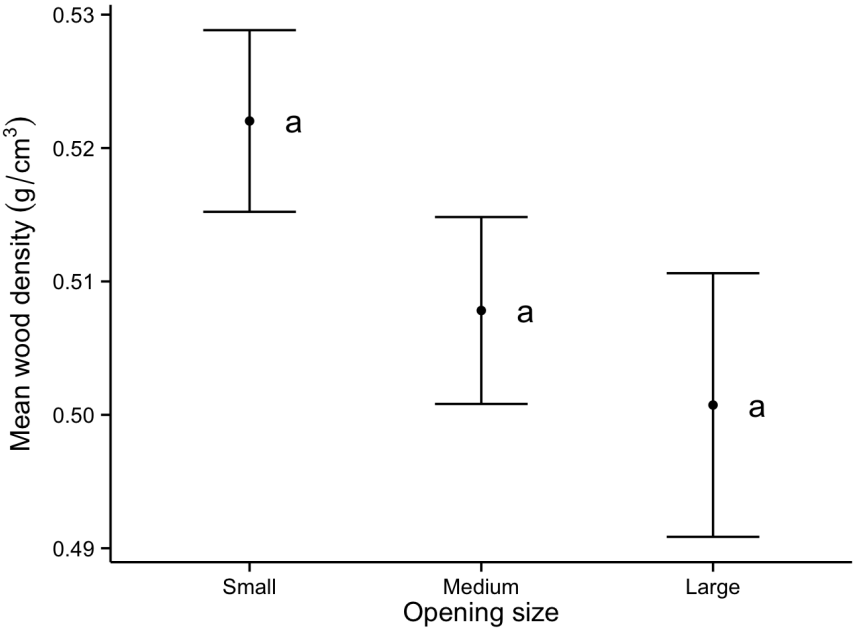

Figure 14. Mean tree wood density by opening size. Letters indicate significant differences. Bars are ± SE.

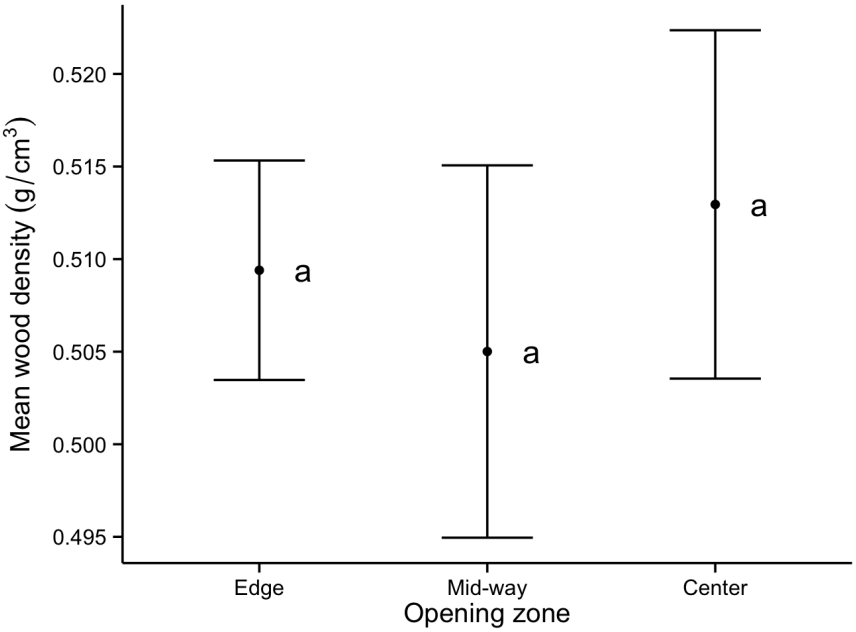

Figure 15. Mean tree wood density by opening zone. Letters indicate significant differences. Bars are ± SE.

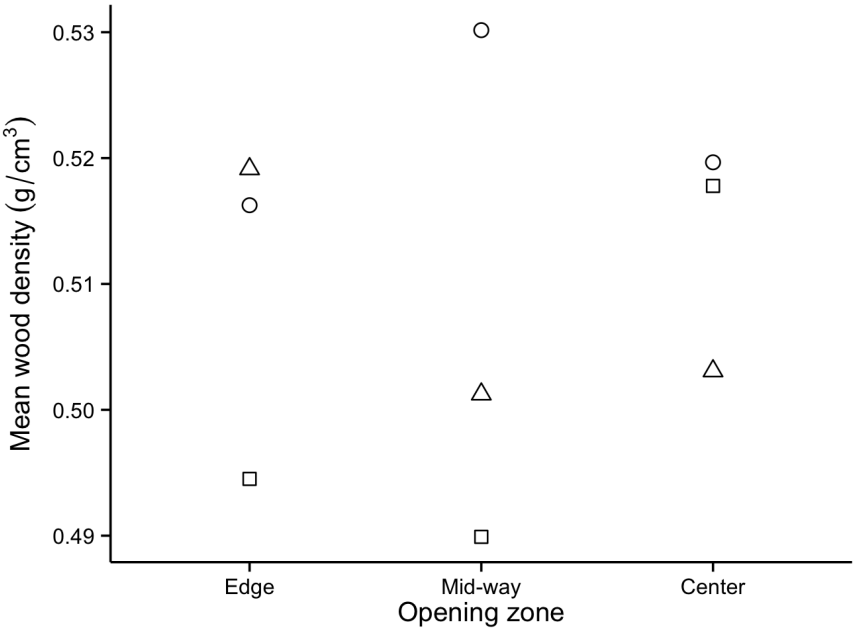

Figure 16. Mean tree wood density by opening zone and size. Shapes are means of different opening sizes. Circles are small openings, triangles are medium, and squares are large.

slightly with openings size from 0.08 to 10.0 ha. However, my results suggest that FHD is not affected by opening size or distance from forest edge on the scale of 2.0 to 14.0 ha. FHD can be affected by the number of height classes chosen (MacArthur and MacArthur 1961). It is possible that using fewer height classes than the six I did would change the results for FHD. Overall, the vertical distribution of vegetation found in my study was consistent with similar aged stands in temperate deciduous forests in the northeastern United States (Aber 1979).

Increasing light levels from the edge to the center of openings and from smaller to larger openings is expected to be associated with increased abundance of intolerant species (Phillips and Shure 1990; York et al. 2003; Baker et al. 2013; Rozman et al. 2015). However, my study did not find any differences in community-weighted mean shade tolerance among different sizes or at different distances from the edge. The smaller openings might not be large enough to create a light environment that would affect the spatial distribution of species based on shade tolerance. However, in openings from 6 to 43 m in diameter, Kern et al. (2013) found that shade tolerance of ground layer vascular plants was lower in larger gaps and in gap centers. Their largest openings had a center-to-edge distance approximately equal to the smallest opening in my study. It is possible that including herbaceous species would show a stronger trend in smaller openings. The leave trees from the shelterwood harvest in my study may have affected the light environment in small and medium openings preventing a trend in shade tolerance with distance from forest edge from developing (Miller et al. 2006). Lienard et al. (2015) reported that community-level shade tolerance can continue to decrease up to 20 years post-disturbance and that it may reach a low point before increasing again with stand age. Thus, across opening sizes, differences in mean shade tolerance based on the effects of differing light environments may not

have had enough time to manifest in the openings in my study.

Wind speeds should be faster in larger openings and farther from the edge (Davies-Colley et al. 2000; Swanson et al. 2011). Greene and Johnson (1993) reported that, among wind-dispersed samara seeds, lighter seeds fell slower than heavier seeds, thus giving the possibility of farther dispersal distance. Additionally, higher seed mass has been shown to confer a competitive advantage in shady conditions, at least in the cotyledon stage (Saverimuttu and Westoby 1996), leading to the expectation that seed mass would be higher near the edge than the center of openings. The lower seed mass found at the center than the edge of openings in my study agrees with this expectation, however seed mass was lower in small openings than in large ones, the reverse of what would be expected based on wind.

The lower seed mass in small openings than in medium and large openings could be the result of differences in species composition in the shrub community rather than differences in dispersal factors among opening sizes. For example, *Pyrularia pubera* has a heavy seed and was one of the most common species in both medium and large openings but was not found in small openings. In small openings two light seeded species (*K. latifolia* and *G. procumbens*) were common, but they were not common in medium or large openings. The distribution of these three species may have been enough to cause the lower seed mass for shrubs in small openings and higher seed mass for shrubs in medium and large openings. It is also possible that sprout regeneration, which was not differentiated from seed origin in my study but has been shown to be prolific in southern Appalachian forests (Shure et al. 2006; Dietze and Clark 2008; Keyser and Loftis 2015), masked the effect of dispersal by light-seeded species because sprouts do not depend on dispersal from outside the opening to establish. Finally, Thomson et al. (2011)

reported seed dispersal distance across 140 species to be strongly correlated with plant height but not seed mass. When plant height was accounted for in their study, lighter seeds had farther dispersal distances but the relationship was very weak; when not accounting for plant height, heavier seeds dispersed farther.

Wood density represents a trade off in resource allocation. Trees with less dense wood have faster growth rates than denser species (Swenson and Enquist 2007), and, in some cases, wood density is positively correlated with shade tolerance (Augspurger 1984). Thus one could expect that larger openings and opening center would have species with less dense wood, because they are able to grow faster and take advantage of higher light levels. However, no significant differences for tree wood density were found among sizes or zones in my study. If there is a spatial effect on wood density related to microclimate, it did not appear in range of opening sizes in my study.

Center-to-edge distances for the small opening size group ranged from 29 to 45 m, meaning that most of the opening would be within one mature tree height of the edge for the common tree species around these openings (USDA, NRCS). A rule-of-thumb definition of edge is one mature tree height into an opening (Bradshaw 1992), and microclimate variables like light, temperature, and soil moisture can be influenced by forest edge for up to 60 m or more (Bradshaw 1992; Baker et al. 2014b; Baker et al. 2016). Thus instead of having a distinct edge and center, small openings in my study may be mostly edge habitat. Within medium openings, which have a range of 75 to 100 m center-to-edge distance, only the center zone begins to escape forest influence. It is possible that openings with a center-to-edge distance of 45 m (the longest for small openings in my study) are not large enough to cause a difference within the woody

plant community in the spatial distribution of shade tolerance, wood density and the vertical structure variables measured here.

Two openings in the study, both in the small size group, were on sites with more ridge-top like conditions with convex topography and species associated with drier sites and lower productivity. While within the classification of *L. tulipifera—Q. alba—Q. rubra* forest type, these openings would be on the drier, less productive side of that classification. This difference could affect the distribution of species found in these sites, as can be seen in the difference between the lists of most common species found in each size group. Smaller openings had more Ericaceous shrubs and dry-site *Quercus* than medium and large openings. Some of these Ericaceous shrubs, such as *K. latifolia,* have very light seeds, which would bring down the mean seed mass for these openings. Light levels on the higher, ridge-top portions of the openings could be higher, affecting the shade tolerance values and raising the community-weighted mean shade tolerance relative to other openings in my study. Differences in productivity could possibly affect the mean height of vegetation at these sites, leading to a lower mean height.

The shade tolerance, seed mass, and wood density of the early seral woody plant community in my openings five to nine years after harvest may be less a result of environmental filters and biotic interactions caused by differences in opening size and distance from forest edge and more a result of the species pool available following a disturbance. Species present right after a disturbance are a legacy of the pre-disturbance forest community, and the arrangement of these species, and thus their traits, in the first decade may be a hold over from that pre-disturbance community (Egler 1954; Franklin et al. 2002; Swanson et al. 2011). Stump sprouting could also add to this effect and dampen the effect opening size and distance from edge

have on the spatial distribution of functional traits in the woody plant community. Leave trees could also be affecting functional trait patterns in two ways. First, the silvicultural prescriptions for these harvests called for leaving hard mast species, which have higher seed mass. Second, leave trees alter the light environment of the opening (Miller et al. 2006), possibly affecting the shade tolerance of regenerating species. This influence on light would also impact the growth of nearby plants and affect vertical structure (Miller et al. 2006).

In conclusion, there does not appear to be a strong effect of opening size on the vertical structure variables (mean height and FHD) or functional traits (shade tolerance, seed mass, and wood density) focused on in my study. Seed mass was the only trait found to differ based on distance from edge. Thus, if regeneration of heavier seeded tree species such as *Quercus* is desired, then consideration of opening size or placement of leave trees should be made. These results have larger implications for forest management. If openings of 60 m in diameter are structurally and functionally similar to openings over 200 m in diameter, then forest managers have a wide range of sizes to choose from in managing for early seral habitat, and several smaller openings may be able to serve the same purpose as few large ones on a landscape level. Further study of functional traits in early seral forest openings could use site specific trait data collected in the field, since data in my study used literature and database species level means. Additionally, the functional traits of the non-woody plant community or other traits related to succession in early seral forests openings of this size range could be investigated.

CHAPTER 4: LITERATURE CITED

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APPENDICES

Appendix A: List of Plant Functional Trait Data Sources

Table A1. List of plant functional trait data sources. Sources are numbered in the table as follows, 1: Niinemets and Valladares 2006; 2: USDA, NRCS; 3: Wilfahrt et al. 2014; 4: Royal Botanic Gardens Kew 2016; 5: Nuss; 6: Plants for a Future; 7: Practical Plants; 8: Univ. of Missouri Extension; 9: Brenek 2016; na: data not used in analyses.

Scientific name	Shade tolerance	Seed mass	Wood density
Tree species			
Acer pensylvanicum L.	1	3	3
Acer rubrum L.	1	3	3
Acer saccharum L.	1	3	3
Aesculus flava Aiton	1	3	3
Amelanchier arborea (Michx. f.) Fernald	1	3	3
Asimina triloba (L.) Dunal	1	3	na
Betula lenta L.	1	3	3
Carya cordiformis (Wangenh.) K. Koch	1	3	3
Carya glabra (Mill.) Sweet	1	3	3
Carya species Nutt.	1[a]	3	3
Carya tomentosa (Lam.) Nutt.	1	3	3
Castanea dentata (Marshall) Borkh.	1	3	3
Cornus alternifolia L. f.	1	2	na
Cornus florida L.	1	3	3
Diospyros virginiana L.	1	2	3
Fagus grandifolia Ehrh.	1	3	3
Fraxinus species L.	1[a]	3[a]	3
Halesia tetraptera Ellis	1	3	3
Ilex montana Torr. & A. Gray ex A. Gray	na	4	na
Ilex opaca Aiton	1	3	3

Scientific name	Shade tolerance	Seed mass	Wood density
Juglans nigra L.	1	3	3
Liriodendron tulipifera L.	1	3	3
Magnolia acuminata (L.) L.	1	3	3
Magnolia fraseri Walter	1	3	3
Nyssa sylvatica Marshall	1	3	3
Oxydendrum arboreum (L.) DC.	1	3	3
Pinus rigida Mill.	1	3	3
Pinus strobus L.	1	3	3
Pinus species L.	1 and 2[a]	3[a]	3
Prunus serotina Ehrh.	1	3	3
Quercus alba L.	1	3	3
Quercus coccinea Münchh.	1	3	3
Quercus falcata Michx.	1	3	3
Quercus montana Willd.	1	3	3
Quercus species L.	1[a]	3[a]	3
Quercus rubra L.	1	3	3
Quercus velutina Lam.	1	3	3
Robinia pseudoacacia L.	1	3	3
Sassafras albidum (Nutt.) Nees	1	3	3
Tilia americana L.	1	3	3
Tsuga canadensis (L.) Carriere	1	3	3
Shrub species			
Aristolochia durior Hill	na	na	na
Calycanthus floridus L.	5, 7, 6	4	na
Epigaea repens L.	7 and 6	4	na
Euonymus americanus L.	1	2	na
Euonymus obovatus Nutt.	na	4	na

Scientific name	Shade tolerance	Seed mass	Wood density
Gaultheria procumbens L.	2	2	na
Gaylussacia ursina (M. A. Curtis) Torr. & A. Gray ex A. Gray	7 and 6	2[c]	na
Hamamelis virginiana L.	1	2	na
Hydrangea arborescens L.	7, 6, 8	2[a]	na
Kalmia latifolia L.	1	2	na
Lindera benzoin (L.) Blume	1	2	na
Lyonia ligustrina (L.) DC.	2	4	na
Parthenocissus quinquefolia (L.) Planch.	2	2	na
Pyrularia pubera Michx.	7 and 6	9	na
Rhododendron calendulaceum (Michx.) Torr.	na	na	na
Rhododendron maximum L.	1	2	na
Rubus allegheniensis Porter	1	2	na
Rubus canadensis L.	1[b]	4	na
Rubus odoratus L.	2	2	na
Rubus species L.	1[b]	2 and 4[a]	na
Smilax glauca Walter	2	4	na
Smilax rotundifolia L.	2	4	na
Symplocos tinctoria (L.) L'Hér	1	4	na
Toxicodendron radicans (L.) Kuntze	7 and 6	4	na
Vaccinium pallidum Aiton	1	4	na
Vaccinium stamineum L.	2	4	na
Viburnum acerifolium L.	2	2	na
Vitis species L.	2[a]	2[a]	na
Vitis rotundifolia Michx.	2	2	na

[a] A composite of two or more congeneric species was used.
[b] Used value for *Rubus allegheniensis*.
[c] Used value for *Gaylussacia baccata* (Wangenh.) K. Koch.

Appendix B: ANOVA Tables for Linear Mixed Models

Table B1. Analysis of variance table for shade tolerance of all species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.018323	0.0091615	2	8	0.27936	0.7634
Zone	0.003205	0.0016027	2	16	0.04887	0.9524
Size:Zone	0.071505	0.0178762	4	16	0.54510	0.7051

Table B2. Analysis of variance table for shade tolerance of tree species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.190902	0.095451	2	8	1.59872	0.2605
Zone	0.033848	0.016924	2	16	0.28347	0.7569
Size:Zone	0.024601	0.006150	4	16	0.10301	0.9798

Table B3. Analysis of variance table for shade tolerance of shrub species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.029014	0.014507	2	8	0.56821	0.5878
Zone	0.027160	0.013580	2	16	0.53191	0.5975
Size:Zone	0.143344	0.035836	4	16	1.40364	0.2775

Table B4. Analysis of variance table for seed mass of all species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.99845	0.49923	2	8	7.4621	0.0148
Zone	0.58294	0.29147	2	16	4.3567	0.0308
Size:Zone	0.03955	0.00989	4	16	0.1478	0.9613

Table B5. Analysis of variance table for seed mass of tree species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.23197	0.115984	2	8	0.98407	0.4149
Zone	0.06281	0.031407	2	16	0.26648	0.7694
Size:Zone	0.82788	0.206969	4	16	1.75603	0.1871

Table B6. Analysis of variance table for seed mass of shrub species.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.60611	0.30306	2	8	4.2408	0.0555
Zone	0.56450	0.28225	2	16	3.9496	0.0403
Size:Zone	0.61415	0.15354	4	16	2.1485	0.1217

Table B7. Analysis of variance table for tree wood density.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.00087731	0.00043865	2	8	0.83078	0.4701
Zone	0.00022251	0.00011126	2	16	0.21071	0.8122
Size:Zone	0.00252909	0.00063227	4	16	1.19748	0.3499

Table B8. Analysis of variance table for mean vegetation height.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.35936	0.179678	2	8	1.3637	0.3093
Zone	0.62642	0.313211	2	16	2.3772	0.1248
Size:Zone	0.37808	0.094521	4	16	0.7174	0.5923

Table B9. Analysis of variance table for foliage height diversity.

	Sum Sq.	Mean Sq.	Num. DF	Den. DF	F	P (>F)
Size	0.135425	0.067712	2	8	1.48997	0.2818
Zone	0.086869	0.043435	2	16	0.95575	0.4054
Size:Zone	0.280447	0.070112	4	16	1.54277	0.2374